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A WEBBED ARCHOSAUR FOOTPRINT FROM THE UPPER TRIASSIC (CARNIAN) OF THE ITALIAN SOUTHERN ALPS

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Abstract—A webbed footprint of Carnian (Tuvalian) age, discovered near Cles (Trentino-Alto Adige, NE Italy), is described. The specimen is compared with other coeval tracks, in particular with those of the Dogna ichnosite (Julian Alps, NE Italy), that are interpreted as preservational variants. The relationship between possible palmate trackmakers and evidence of webbing in the tracks are discussed. The trackmaker is interpreted as a quadrupedal crocodylomorph showing possible aquatic adaptations.

INTRODUCTION AND GEOLOGY

Here we report the discovery of some unusual archosaur footprints near Cles village, about 48 km north of Trento (Trentino-Alto Adige, NE Italy) (Fig. 1). The footprint-bearing layer belongs to the Travenanzes Formation (= upper portion of the "Raibl Beds" Auct.; Neri et al. 2005), which is of late Carnian (Tuvalian) age (see also Avanzini et al., 2009). This formation consists mainly of interbedded white-gray aphanitic to silty dolostones and reddish or greenish shales. The sedimentary succession has been interpreted as representing a marginal marine environment with supplies of terrigenous or fully marine, albeit shallow, sediments (Gennaro, 2007; D'Orazi et al., 2008).

MATERIAL

The footprints are generally poorly preserved as convex hyporeliefs on a dolostone layer, covered by a thin reddish marly layer. The original trampled layer (with the true tracks) was a marly, cm-thick level that was lost during the excavation. The true tracks were left in sediment that was very wet and soft. Most prints are fairly shallow, and generally deeper distally and shallower in the palm or heel. None of the observed prints could be placed in manus-pes sets or trackways. Only one specimen (MTSN 5648), now stored at the Museo Tridentino di Scienze Naturali, is moderately well preserved, showing some peculiar morphological features described here.

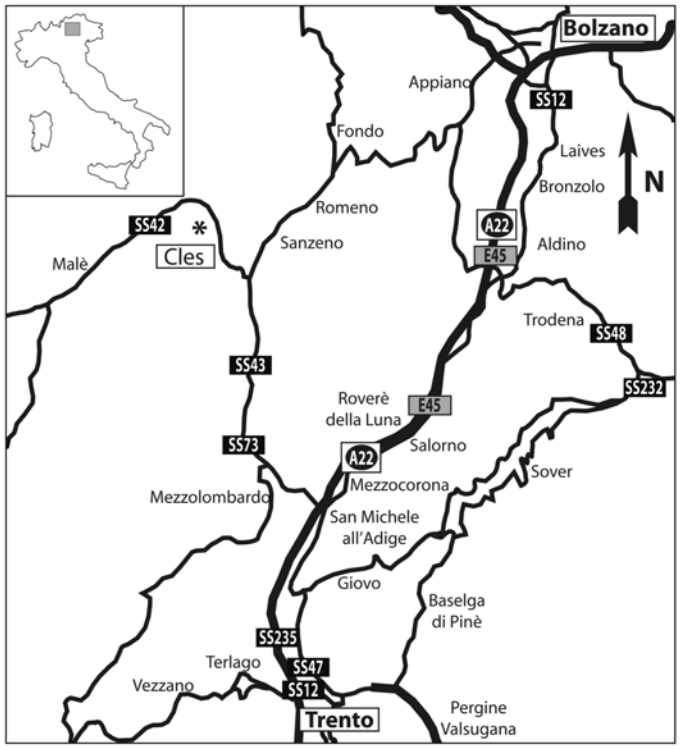

FIGURE 1. Locality map showing the Cles site (Trentino-Alto Adige, NE Italy).

DESCRIPTION

Only the pes imprint is preserved. It is pentadactyl, semi-plantigrade and longer than wide (length/width ratio ~ 1.4; Fig. 2A). Digit group I-IV is as long as wide, and the single digits are short and narrow. Digit III is the longest, while digit II may be longer than digit IV or have the same length. Digit V is represented only as a broad pad impression, elliptical in shape, postero-laterally positioned and almost in line with the long axis of digit IV. The angle between digits I-IV is 50°. The interdigital angle (IDA) I-II and II-III is roughly equal (~ 20°), while III-IV is wider (~ 24°). Digit impressions I-III taper distally, suggesting the presence of claws. Phalangeal nodes are preserved along digits I, II and IV. An expulsion rim borders the distal portion of digits I-IV. In the area between the expulsion rim and the hypices of digits II-III and III-IV, poorly preserved skin impressions are recognizable. They are arranged in aligned rows of mm-sized, sub-rounded tubercles (see discussion; Fig. 2B-C).

Parameters: Footprint length (L) 150 mm; footprint width (W) 110 mm; digit lengths ~65 mm (I), ~70 mm (II), ~75 mm (III); ~70 mm (IV).

DISCUSSION

Pedal morphology and geological age strongly suggest a crurotarsan archosaur as the best candidate trackmaker. The general morphology of the pes reminds one of crocodylians (Fig. 3). As in living crocodylians and in some early crocodylomorphs, the pes shows four distinct digits (Farlow and Elsey, 2010). Nevertheless, early crocodylomorphs were mainly gracile and possibly bipedal animals (Carroll, 1988). The stratigraphically oldest is Norian in age (Benton, 1994), and the oldest ichnological record of true crocodylomorph trackmakers comes from Early Jurassic strata (Olsen and Padian, 1986).

Phytosaurs (Parasuchia) were morphologically very similar to crocodilians and reached their maximum diversification and distribution during the Carnian-Norian interval. However, they show a clawed foot with five well-developed digits, in which digit IV is the longest (Parrish, 1986). When preserved (*Pseudopalatus pristinus:* Long and Murry, 1995; *Parasuchus hislopi* and *Rutiodon tenuis*: Parrish, 1986), digits V and I are nearly at the same height along the lateral and medial margins of the foot, and digit V is less reduced compared with the condition in crocodylomorphs. This feature is evident in the supposed *Rutiodon* pedal print described by Parrish (1986) but not in the footprint de-

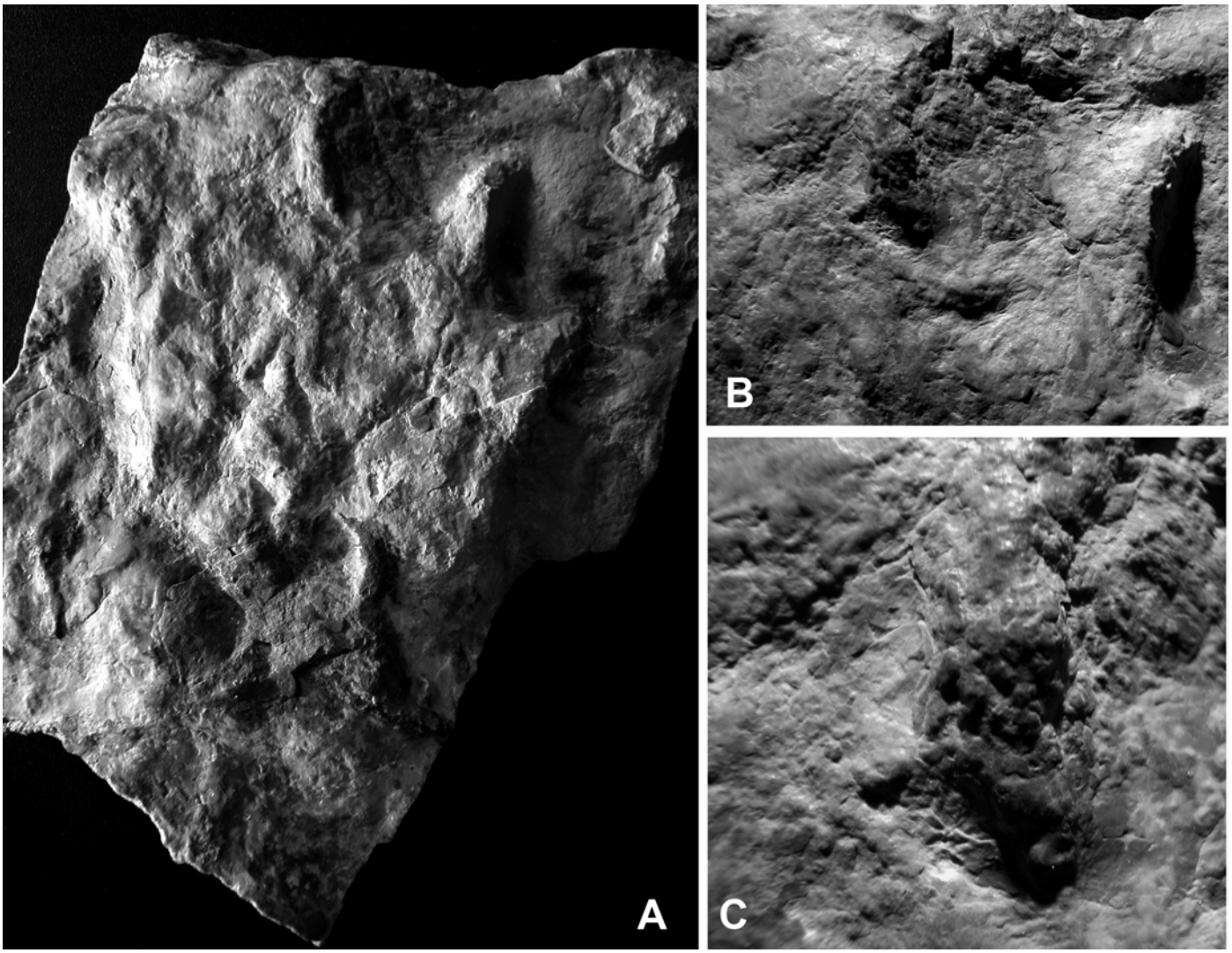

FIGURE 2. **A**, MTSN 5648, right pedal imprint; **B-C**, successive magnifications of the interdigital webbed area between digits II-III where aligned rows of mm-sized subrounded tubercles are visible.

scribed here. *Apatopus lineatus* (Bock 1952) is the only ichnospecies so far attributed to phytosaurs. The ichnogenus *Apatopus* described by Baird (1957) substantially differs from our footprint by the occurrence of a well developed digit V, by digit IV being longest, and by the generally less chirotheriid shape of digit group I-IV.

Avanzini et al. (2010) reported the discovery of several archosaur footprints attributed to *Brachychirotherium eyermani* (Baird, 1957) from the same locality and stratigraphic level of MTSN5648 (but not from the same layer). Those, however, show broad digits, a well impressed and oval-shaped heel, no evidence of webbing and generally different track parameters, making unprobable any relationhip between the two finds. The above reported morphological characters are sufficiently diversified to exclude a track preservational variant related to substrate properties.

The only comparable footprints from the Upper Triassic of Southern Alps were discovered in the Carnian of Dogna (Julian Alps, Friuli Venezia Giulia) (Dalla Vecchia, 1996; Avanzini et al., 2007) (Fig. 4). Pedal imprints from the Dogna site are plantigrade, 17-20 cm long, narrow and elongate in shape, wider anteriorly and relatively symmetrical, with five short and narrow digits. Digit III is the longest, digit I is the shortest, and digits II and IV are subequal in length. The very shallow digit V mark, visible in a few footprints, is short, thin, situated postero-laterally and is antero-laterally oriented. The evidence suggests that the trackmaker was a quadruped with an erect stance and relatively efficient gait, like that of fast-walking crocodiles (Dalla Vecchia, 1996; Roghi and Dalla Vecchia, 1997). Dalla Vecchia (1996) and Roghi and Dalla Vecchia (1997) suggested an archosaur, possibly an aetosaur, as the candidate trackmaker (see also Avanzini et al., 2007). MTSN5648 and the footprints from Dogna show the same general morphology, and both are strongly controlled by the substrate consistency. The Cles trackmaker was, however, probably moving on a plastic mud layer.

The presence of possible webbing in the Dogna footprints was first suggested by Dalla Vecchia (1996) who, however, was not able to provide evidence of that because of the poor preservation of the specimens. The possible presence of interdigital webbing is a topic of long-standing debate in vertebrate palaeoichnology. Recently, Falkingham et al. (2009) have clearly shown that "webbing" can result from interaction with the sediment and not necessarily as a consequence of direct impression of a webbed foot. Bearing this in mind, we here provide several arguments in favor of our interpretation of a webbed trackmaker for the here-described footprint. If our interpretation is correct, most of these can be applied also to the Dogna footprints.

The most convincing evidence is the presence of skin impressions just above the hypices between digits II-III and III-IV (Fig. 5). Skin impressions are constituted of small patches of tiny sub-rounded tubercles aligned in rows. Similar structures are also visible in the median part of the pedal impression but not on the surface of the slab outside the

FIGURE 3. Right pes of a modern alligator. Specimen RWR 26, Rockefeller Wildlife Refuge, Louisiana. From Farlow and Elsey (2010), this volume.

footprint, giving support to the interpretation of the structures as skin impressions and not as a result of physical processes (e.g., degasification structures). Falkingham et al. (2009) have shown that false-webbing (i.e., the sedimentary structure) forms only at a specific interdigital angle, and that as the angle increases, the size of this structure decreases. This is the opposite of what we observe in the here-described specimen: the webbed structure is present between digits I-II, II-III, with digits III-IV showing different IDAs. Furthermore, the widest webbed structure is present between digits III-IV where also the IDA is the widest. Notably, this asymmetric development of the webbed surface (IV-III > III-II ? II-I) is similar to those seen in modern crocodiles (Fig. 3). In addition, the interdigital structure erroneously described as webbing by Lockley and Meyer (2004) and discussed by Falkingham et al. (2009) appears as a "platform" when viewed in profile. On the contrary, those seen in MTSN5648 show a marked steepening in the profile curve that permits us to clearly discern the webbing from the expulsion rim. Furthermore, the latter contours the digit I-IV impressions following a path that would be hardly understandable if not hypothesizing a webbed trackmaker.

CONCLUSIONS

The Cles tracksite reveals some of the best- preserved archosaur tracks from the Upper Triassic (late Carnian) of the Southern Alps (see also Avanzini et al., 2010). The pedal imprint (MTSN5648) discussed in this paper is very comparable to the unnamed archosaurian footprints described by Dalla Vecchia (1996) from the Dogna site (Julian Alps) and whose morphological features were likely controlled by substrate properties such as consistency and water content. The footprint was produced by a quadrupedal trackmaker with a slender, pentadactyl, elongated foot. The trackmaker was a quadrupedal crurotarsan archosaur, probably a crocodylomorph with aquatic adaptations.

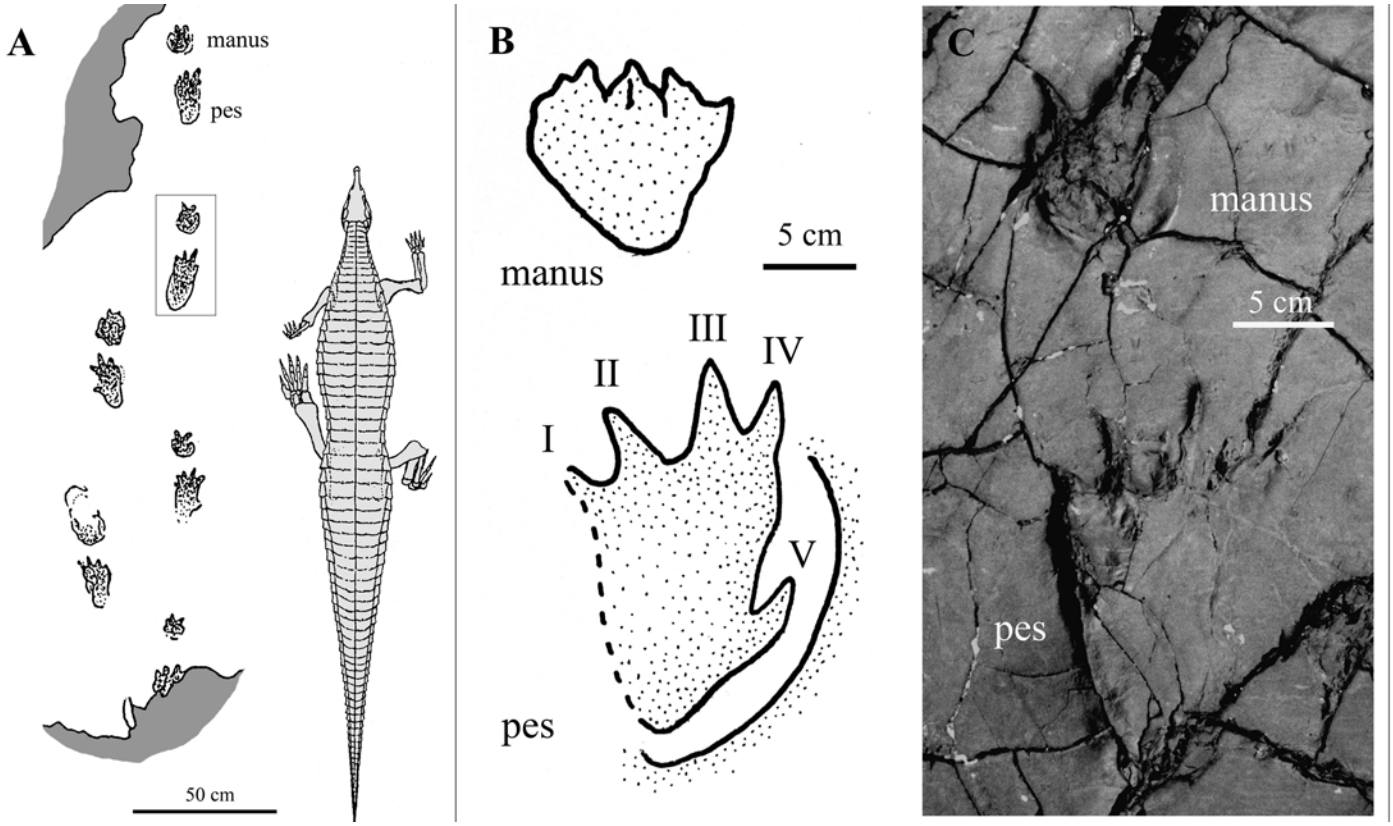

FIGURE 4. Dogna trackways and footprints, from Avanzini et al. (2007) mod. **A**, Dogna Trackway A and possible trackmaker, an aetosaur. **B**, Right manus-pes set from Dogna trackway B. **C**, Right manus-pes set from Dogna trackway A (shown in **A**). Morphology of Dogna tracks as well as the one described in this article may have been strongly controlled by substrate properties and may represent the same ichnotaxon.

FIGURE 5. Interpretive drawing of MTSN 5648 specimen. Shaded areas highlight interdigital webbing, round circles indicate skin tubercles, row of dots and "+" indicates the expulsion rim.

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